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Survival and extinction in the replicator model: Dynamics and statistics

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We study the multi-species replicator model with linear fitness and random fitness matrices of various classes. By means of numerical resolution of the replicator equations, we determine the survival probability of a species in terms of its average interaction with the rest of the system. The role of the interaction pattern of the ecosystem in defining survival and extinction probabilities is emphasized.

Keywords: Replicator dynamics; ecosystem models; survival strategy

1. Introduction

Consider an ecosystem formed by N biological species, with populations n_1, \dots, n_N . Over time scales where the effect of mutations can be neglected, the population of species i is governed by the evolution equation

$$\dot{n}_i = f_i n_i, \quad (1.1)$$

where f_i is the (Fisherian) fitness of that species [3,8]. Equation (1.1) assumes that evolution is continuous in time and that populations are large enough as to neglect the effect of random drift [9]. The interaction between species in the ecosystem is described by the fitnesses f_i , which generally depend on the whole set of populations. They may also include the effect of migration from and toward the system. It can be straightforwardly shown that the frequency of species i in the whole population, $x_i = n_i / \sum_j n_j$, satisfies the evolution equation

$$\dot{x}_i = x_i \left(f_i - \sum_j x_j f_j \right). \quad (1.2)$$

Assuming that the fitnesses can be given as functions of x_1, \dots, x_N gives a closed set of equations for the frequencies, usually referred to as the *replicator equations* [6].

Note that the replicator equations admit an alternative interpretation as the evolution equations for the populations –instead of the frequencies– of an N -species ecosystem. Since for all times $\sum_i x_i = 1$ (see also Sect. 2), this would correspond to an ecosystem with fixed total population, presumably saturating the carrying capacity of its environment. Within this interpretation, thus, the replicator equations describe an ensemble of biological species with global competition, which limits the growth of the whole population to the carrying capacity of the environment, and subject to interactions that affect the individual fitnesses.

The replicator model has found many applications in biological evolutionary problems at various levels. It has been first considered in connection with the evolution of biomolecular concentrations in the early stages of life on the Earth [2]. In the frame of game theory, in close connection with biological evolution [7], it has been used to describe the dynamics of strategy frequencies in multi-player games [13]. As a basic model of an ecosystem, it was discussed by Schuster and Sigmund [12], who coined the term *replicator*. The discrete-time version of Eqs. (1.2) [11] constitutes a well-known model for the evolution of genetic frequencies in asexual haploid populations [9]. Most of these applications assume that the fitnesses depend linearly on the frequencies, $f_i = \sum_j a_{ij}x_j$, so that the replicator equations reduce to

$$\dot{x}_i = x_i \left(\sum_j a_{ij}x_j - \sum_{j,k} a_{jk}x_jx_k \right). \quad (1.3)$$

The matrix $A = \{a_{ij}\}$ is frequently called *fitness matrix* and, from the viewpoint of game theory, plays the role of a payoff matrix. It can be shown that the replicator equations with linear fitness are formally equivalent to a multi-species Lotka-Volterra model [6].

In spite of the large potential of the replicator equations to model evolutionary biological systems, the dynamical properties of their solutions are poorly understood. Besides the specific applications quoted above, generic mathematical properties of the replicator model are known for very special situations only [6,14]. Typically, they involve a small number of biological species with quite unrealistic interaction patterns. Real ecosystems, on the other hand, usually involve tens of species with hundreds of food-web links [5,4]. Our aim in this paper is to approach this complex reality by exploring the replicator dynamics for large ecosystems with nontrivial interaction patterns. We deal with the problem from a statistical point of view and perform extensive numerical calculations, focusing on a probabilistic description of survival and extinction of species in terms of the parameters that define their interaction.

In the next two sections we present –mainly for completeness and subsequent reference– various, rather general mathematical properties of the replicator equations, including symmetry properties and stability conditions for special classes of random interaction patterns. Then, in the main part of the paper, we numerically

study more complex situations for the case of linear fitness, including multi-diagonal and disordered fitness matrices. Our results, which we interpret in connection with the average interaction of each species with the rest of the ecosystem, are summarized and discussed in the last section.

2. Invariance properties and symmetries

For future reference, let us begin discussing the invariance properties of the replicator model (1.2). In the first place, since the variables x_i are defined as population fractions, $x_i = n_i / \sum_j n_j$, the conditions $x_i \geq 0$ and $\sum_i x_i = 1$ must hold at all times. Equations (1.2) are compatible with these conditions, because the set $S_N = \{\mathbf{x} = (x_1, \dots, x_N) / x_i \geq 0 \ \forall i \text{ and } \sum_i x_i = 1\}$ is invariant under their action. In fact, the transverse component of $\dot{\mathbf{x}}$ vanishes on the boundary of S_N , and

$$\sum_i \dot{x}_i = \left(1 - \sum_i x_i\right) \sum_j x_j f_j \quad (2.1)$$

identically vanishes in S_N . Consequently, an initial condition in S_N generates a trajectory which remains within this set. From now on, we restrict the analysis of Eqs. (1.2) to S_N , where the dynamics is effectively $N - 1$ -dimensional. In fact, S_N is an $N - 1$ -dimensional polyhedron embedded in the N -dimensional Euclidean space.

Equations (1.2) have moreover two important symmetries. First, multiplication of all the fitnesses by the same constant $f_i \rightarrow c_1 f_i$, is equivalent to a linear change of the temporal scale, $t \rightarrow c_1 t$. Second, addition of the same constant to all the fitnesses, $f_i \rightarrow f_i + c_2$ leaves the equations invariant. This second symmetry implies that any meaningful result regarding the replicator dynamics will be given in terms of differences between fitnesses, rather than in terms of their individual values. Note, in fact, that Eqs. (1.2) can be rewritten as

$$\dot{x}_i = x_i \sum_j (f_i - f_j) x_j. \quad (2.2)$$

For linear fitness, Eqs. (1.3), the above symmetries respectively amount to multiplying and adding a constant to each element of the fitness matrix A , $a_{ij} \rightarrow c_1 a_{ij}$ and $a_{ij} \rightarrow a_{ij} + c_2$.

3. Linear fitness: Ecological attitude and behavior

In the following, we focus the analysis on the case of linear fitness, $f_i = \sum_j a_{ij} x_j$. For the sake of simplicity, the restriction of Eqs. (1.3) to S_N will be referred to as the replicator equations.

The two summations in the right hand side of Eqs. (1.3) couple the dynamics of the species in different ways. The first summation, $\sum_j a_{ij} x_j$, coincides with the fitness of species i , and is a direct measure of the effect of the whole ecosystem on the reproductive success of that species. The coefficient a_{ij} , in fact, weights the contribution of species j to the fitness of i . The second summation, $\sum_{kl} a_{kl} x_k x_l$ is

the average fitness in the ecosystem, and acts as a global coupling. This “interaction” –a negative contribution for positive a_{kl} – is responsible for the preservation of the normalization of $\sum_i x_i$. The invariance of the system under summation of a constant to the fitness, quoted in Sect. 2, implies that all dynamical features in the replicator model depend on the fitness matrix A through differences between its elements. As a matter of fact, we find that a set of relevant quantities in the characterization of such features is given by the differences $g_{ij} = a_{ij} - a_{jj}$. They compare the contribution of species j to the evolution of i with its self-contribution. We call g_{ij} the *attitude* of species j toward species i . A positive attitude, $g_{ij} > 0$, indicates that species j contributes to the growth of i more than to its own growth. It is therefore an *altruistic* attitude. On the other hand, $g_{ij} < 0$ stands for an *egoistic* attitude. By definition, the “self-attitudes” g_{jj} are all zero. As we show in the following, the stability properties of many of the equilibria of Eqs. (1.3) can be given in terms of the attitudes g_{ij} .

For large N , Eqs. (1.3) have generally a large number of fixed points. They can be classified by their number of non-vanishing coordinates, i.e. by the number of surviving species at each fixed point. There are N fixed points with only one surviving species. The coordinates of these points are all zero except that corresponding to the surviving species, which equals unity. We emphasize that such equilibrium points, situated at the *vertices* of S_N , always exist, independently of the values of the coefficients a_{ij} . In contrast, the number of fixed points with n surviving species ($1 < n < N$) depends on a_{ij} . We do know, however, that $C(N, n) = N!/n!(N-n)!$ is an upper bound for this number. These equilibrium points lie on the *edges* of the polyhedron S_N . Finally, only one equilibrium with N surviving species can exist [6]. We call it the *coexistence* fixed point. If it exists, its coordinates satisfy $\sum_j a_{ij}x_j = \sum_{kl} a_{kl}x_kx_l$ for all i .

For a general fitness matrix A and arbitrary N , the linear stability analysis of the fixed points of the replicator equations is quite a difficult task. Still, it is possible to find the general stability conditions for vertices. The j -th vertex, with $x_j = 1$ and $x_i = 0$ for all $i \neq j$, is linearly stable if and only if $g_{ij} < 0$ for all $i \neq j$, i.e. if species j is egoistic toward all other species. Note that this condition can be simultaneously verified for several –or even all– species, in which case the system is multistable.

An important case where the stability analysis can be fully achieved for all the fixed points is that of a diagonal matrix ($a_{ij} = 0$ for $i \neq j$), which will be used as a reference case in our statistical analysis of survival and extinction. In this case, as above, the j -th vertex is linearly stable if and only if $g_{ij} < 0$ or, equivalently, $a_{jj} > 0$. The equilibria on the edges of S_N , on the other hand, are always unstable. Meanwhile, the coexistence point is stable if and only if $g_{ij} = -a_{jj} > 0$ for all i , i.e. if all species are altruistic toward all other species. Consequently, if the coexistence point is stable, it is the only stable equilibrium, since the vertices are in turn unstable. The global stability of the coexistence point follows also from a general theorem for the replicator system with symmetric fitness matrices [6].

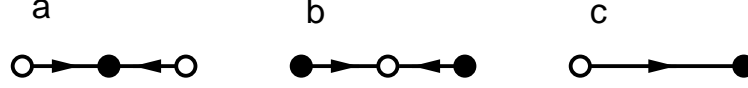


Fig. 1. Dynamical behaviors for a two-species system: (a) coexistence, (b) bistability, and (c) domination by one species. In the three cases, empty dots indicate unstable fixed points, while full dots indicate stable equilibria.

Linear stability analysis can also be carried out explicitly for small values of N . For two species, the dynamics is effectively one-dimensional. The phase space S_2 can be mapped onto the interval $[0, 1]$, where one of the variables (say x_1) takes on its values, while $x_2 = 1 - x_1$ at all times. In Fig. 1 we sketch the three possible dynamical scenarios. Coexistence (Fig. 1a) occurs when both species have positive attitude toward each other, while bistability (Fig. 1b) occurs when both species have negative attitudes. Domination by one of the species takes place when one species is altruistic and the other species is egoistic. In such case the egoistic species dominates, while the other becomes extinct. For three species the dynamics is effectively bidimensional, and there is a wider spectrum of dynamical behaviors, including the possibility of existence of heteroclinic cycles [6]. In general, we find that stability properties depend not only on the signs of the attitudes g_{ij} , but also on other combinations of the elements a_{ij} .

Real ecosystems, however, are known to involve at least several species with complex patterns of interactions [5,4]. The restricting conditions that make the replicator model analytically solvable fall well apart from any situation with biological significance. We therefore turn our attention to many-species systems with nontrivial interactions. In order to explore an ample class of fitness matrices, we choose the elements a_{ij} at random, from prescribed distributions. This choice calls for a statistical analysis of the results, which in turn require resorting to the numerical resolution of the replicator equations. In the next section we discuss methods and present results of such analysis.

4. Random fitness matrices for many-species ecosystems

As advanced above, we analyze in this section the dynamics of the replicator model with a random fitness matrix and for a large number of species. In a generic situation, the coexistence equilibrium will be unstable and a substantial number of species will become extinct. We are particularly interested in studying the dependence of the number of surviving species on the distribution of the elements a_{ij} . Our ultimate goal would be to identify the ecological attitude that a species should have in order to optimize its probability of surviving within a given population, i. e. for a given distribution of a_{ij} . From then on, in order to make the description of interactions more compact, we characterize a species j by its mean attitude

$$G_j = \frac{1}{N} \sum_i g_{ij} = \frac{1}{N} \sum_i (a_{ij} - a_{jj}). \quad (4.1)$$

Depending on the distribution of a_{ij} , the mean attitudes in a given population will take values in different ranges. For each realization of the evolution of the system, we respectively call $n(G)$ and $n_s(G)$ the (normalized) distribution of the number of species and of the number of surviving species on G . Namely, for small δG , the products $Nn(G)\delta G$ and $Nn_s(G)\delta G$ represent, respectively, the total number of species and the number of surviving species in the interval $(G, G + \delta G)$. The average fraction of surviving species as a function of the mean attitude is given by

$$\rho(G) = \frac{\langle n_s(G) \rangle}{\langle n(G) \rangle}, \quad (4.2)$$

where $\langle \cdot \rangle$ indicates average over realizations, with different a_{ij} and different initial conditions. The product $\rho(G)\delta G$ measures the survival probability of a species with mean attitude between G and $G + \delta G$ within the given population.

Taking into account the symmetries of the replicator equations (1.3), discussed in Sect. 2, we have selected a set of distributions for a_{ij} that results to be representative and interesting. In most cases, we fix a significant subset of the matrix elements equal to zero, while the remaining a_{ij} are uniformly distributed on a finite interval. The subset of null elements can be fixed deterministically or at random over the matrix, and defines a reference level for all the other a_{ij} . Three intervals for the uniform distribution of the nonzero elements will be considered, namely, $(-\frac{3}{2}, -\frac{1}{2})$, $(-\frac{1}{2}, \frac{1}{2})$, and $(\frac{1}{2}, \frac{3}{2})$. In this way, we take into account translations of the distribution of the nonzero elements with respect to the reference value. Note that, on the other hand, the three intervals have the same width. We briefly discuss the effect of changing this width at the end of Sect. 4.3.

A special reference case which will also be considered in the following is a fitness matrix where no element is *a priori* fixed to zero, and a_{ij} is chosen from the uniform distribution for all i and j . This special case is statistically invariant under translations of the interval and changes of its width –up to a modification in the time scale.

4.1. Numerical calculations

In the numerical resolution of the replicator equations we face a main difficulty, namely, the dynamical instability of the invariant set S_N . From Eqs. (2.1) it follows that, depending on the sign of the global coupling term $\sum_j x_j f_j = \sum_{j,k} a_{jk} x_j x_k$, a small perturbation on the condition $\sum_i x_i = 1$ may be amplified by the dynamics, driving the system away from S_N . This is expected to happen in the numerical calculations, due to rounding-off and discretization effects. Using a second-order Runge-Kutta (RK) integration algorithm [10], we have observed departures from S_N for very long times only, typically when the evolution is very slow and the system is close to an unstable fixed point. However, such events prompt us to modify the integration algorithm, in order to ensure permanence on S_N at all times. To solve the problem, we have included a normalization operation at each time step. After computing the updated variables $x_i(t + dt)$ using the RK algorithm, we compute

the sum $\sigma = \sum_i x_i(t+dt)$ and renormalize the variables as $x_i(t+dt) \rightarrow x_i(t+dt)/\sigma$. We have exhaustively tested this algorithm and observed that, in the regions where the original RK algorithm does not produce divergences, the solutions by both methods are indistinguishable. Furthermore, for the original RK algorithm we have observed that the perturbations that drive the solution away from S_N are initially of the order of the working precision ($\sim 10^{-16}$), and the corrections introduced by the normalization procedure are of the same order, or $\sim 10^{-15}$ at most. Such modifications are therefore much smaller than the discretization error of the RK algorithm, and the effect of normalization on the numerical precision results to be negligible.

We have chosen initial conditions for x_i with uniform distribution over S_N . They have been generated by drawing $N - 1$ uniformly distributed random numbers y_i in $(0, 1)$, with $y_1 < y_2 < \dots < y_{N-1}$, and defining $x_i(0) = y_{i+1} - y_i$ for $1 \leq i < N$ and $x_N(0) = 1 - y_{N-1}$.

After integration over sufficiently long times, the values of x_i corresponding to the species which are in the way of becoming extinct have typically reached extremely low levels. Such levels are usually meaningless from the biological viewpoint. In fact, the discreteness of biological populations fixes a lower bound of $(\sum_j n_j)^{-1}$ for each x_i [1]. Since the replicator model does not keep trace of the total population in the ecosystem, we choose as a threshold for extinctions $x_{\min} = 10^{-3}/N$. If, at the end of the integration, a variable x_i has reached a value below x_{\min} , species i is considered to have undergone extinction. To study the evolution of the number of surviving species, this definition is extended to all times. Surviving species at time t are hence defined as those for which $x_i(t) > x_{\min}$. Our value of x_{\min} is essentially arbitrary, but we find that the results are robust with respect to variations in this extinction threshold.

Our calculations correspond mostly to the case $N = 32$, though we have verified that our main qualitative conclusions are valid for considerably larger ecosystems. As indicated above, our statistical analysis requires to average results over realizations with different initial conditions and different matrix elements. Averages were taken over sets of 900 to 6000 realizations. In the following, we present the main results of our analysis, which focuses on the evolution of the number of surviving species and on the determination of the survival probability as a function of the mean attitude of each species.

4.2. Diagonal and full-matrix systems

We begin by analyzing, as a reference situation, the case of a diagonal fitness matrix ($a_{ij} = 0$ for $i \neq j$). Recall that the stability properties in this case can be worked out exhaustively (Sect. 3). Note also that, for the diagonal system, $g_{ij} = -a_{jj}$ is independent of i , such that the attitude of each species j toward the remaining species is uniform.

When the diagonal elements are drawn at random from the interval $(-\frac{3}{2}, -\frac{1}{2})$,

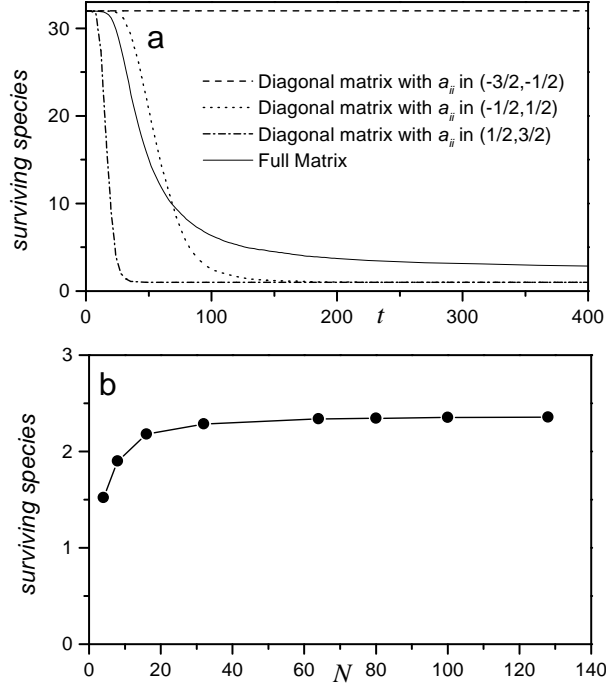


Fig. 2. (a) Number of surviving species as a function of time for diagonal fitness matrices and for the full-matrix case, with nonzero elements uniformly distributed on the indicated intervals. (b) Long time limit of the number of surviving species in the full-matrix case as a function of N .

all these elements are negative. In this case all the species are altruistic, the coexistence point is globally stable, and all the species survive. The survival probability $\rho(G)$ is thus a flat distribution. In the case that the diagonal elements are drawn from $(-\frac{1}{2}, \frac{1}{2})$, typically half of the species –those with $a_{jj} < 0$ – are altruistic toward any other species, while the other half are egoistic. The only stable equilibria are the approximately $N/2$ vertices corresponding to the survival of a single species with $a_{jj} > 0$. The surviving species is selected, in each realization, by the initial condition. Finally, when the diagonal elements are chosen from $(\frac{1}{2}, \frac{3}{2})$, all the species are egoistic and the N vertices are stable. These are again the only stable equilibria and only one species survives. Figure 2a shows the evolution of the average number of surviving species for the above three cases. The corresponding survival probability distributions $\rho(G)$ will be discussed later on, for comparison with other random matrices.

A second case of reference is given, as advanced above, by the situation where no elements of the fitness matrix are *a priori* fixed to zero. We refer to this situation as the full-matrix case. The evolution of the average number of surviving species for the full-matrix case is also shown in Fig. 2a. It is interesting to point out the relatively low number of species that ultimately survive in this case, which for 32

species is around 2.28 on the average. In Fig. 2b we show the average number of surviving species for the full-matrix system as a function of N . It does not change significantly with N , since for $N = 128$ it is around 2.35. As for the diagonal matrix, the distribution $\rho(G)$ for the full-matrix case will be presented later.

4.3. Systems with multi-diagonal matrices

Taking the diagonal-matrix and the full-matrix systems as limiting reference cases, we now study intermediate, more complex situations. We consider Eqs. (1.3) for matrices with different numbers of nonzero diagonals. We define a k -diagonal random matrix, with k an odd natural number, as a matrix whose elements a_{ij} vanish for $|i - j| > (k - 1)/2$ and which are otherwise taken at random from a given distribution. Clearly, $k = 1$ corresponds to the diagonal matrix, while the full-matrix case corresponds to $k = 2N - 1$.

Figure 3a shows the evolution of the mean number of surviving species for multi-diagonal matrix systems with several values of k , and with the nonzero elements distributed uniformly on the interval $(-\frac{3}{2}, -\frac{1}{2})$. It can be seen that the average number of extinctions rapidly increases with the number of nonzero diagonals. In Fig. 3b we show the average normalized distribution of mean attitudes $\langle n(G) \rangle$ for three of the five cases analyzed in Fig. 3a. The range of mean attitudes where $\langle n(G) \rangle$ is sensibly different from zero moves toward the left as k is increased, reflecting the fact that the number of egoistic species grows. Combining this observation with the results of Fig. 3a we conclude that the more egoistic the population is, the less the number of surviving species.

In Fig. 3c we show the numerical result for $\rho(G)$ in the same realizations of Fig. 3a. Since in the diagonal-matrix case ($k = 1$) all the species survive, $\rho(G)$ corresponds to a uniform distribution. The results for $k = 3$ and $k = 7$ are remarkably different. The survival probabilities are in general lower than in the diagonal-matrix case and decrease almost linearly with the mean attitude over a wide range of values of G . Near the ends of the relevant intervals the linear behavior breaks down, and $\rho(G)$ shows abrupt maxima. The maximum on the left side of the intervals indicate that, as expected, being one of the most egoistic species is a good strategy, as far as survival is concerned. Less obviously, the rightmost maximum indicates that being one of the most altruistic species is also convenient for survival. For $k = 15$, $\rho(G)$ does not attain a maximum on the left extreme of the relevant interval and an intermediate optimum value of the mean attitude, close to $G = 0$ appears, instead.

In Figs. 4 and 5 we present the results for multi-diagonal matrices with their non-vanishing elements distributed uniformly on $(-\frac{1}{2}, \frac{1}{2})$ and $(\frac{1}{2}, \frac{3}{2})$, respectively. In these situations, the population is more egoistic than in the case of Fig. 3, and the number of surviving species is very small. In contrast with that case, the number of survivals in the diagonal-matrix system is lower than for the full-matrix system. Now, only one species survives for a diagonal matrix, and the full-matrix case appears to be the situation with the highest rate of survivals. In the case of Fig. 4,

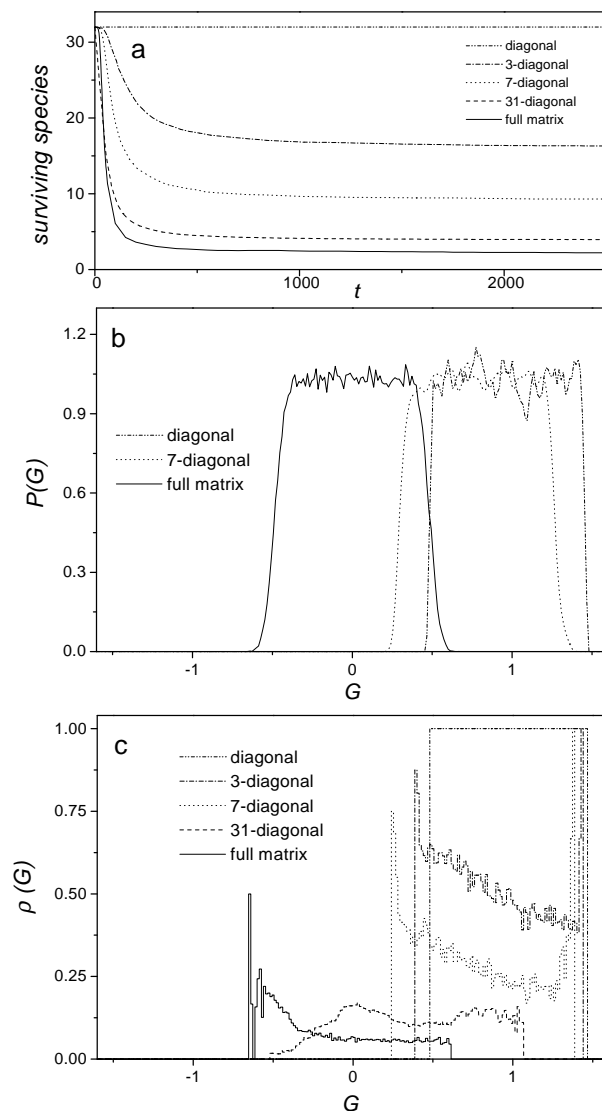


Fig. 3. (a) Number of surviving species as a function of time, (b) distributions of mean attitudes $P(G)$, and (c) survival probability $\rho(G)$, for multi-diagonal fitness matrices with nonzero elements taken from a homogeneous distribution on $(-\frac{3}{2}, -\frac{1}{2})$.

the transition between the limiting situations is smooth: the profiles of $\rho(G)$ for different values of k are similar. All of them decrease monotonically with the mean attitude for intermediate values of G , and present abrupt maxima at the ends of the relevant intervals. The situation in Fig. 5 is more complex, and somehow more similar to the case of Fig. 3, since a maximum of ρ for an intermediate value of G is observed for relatively high values of k .

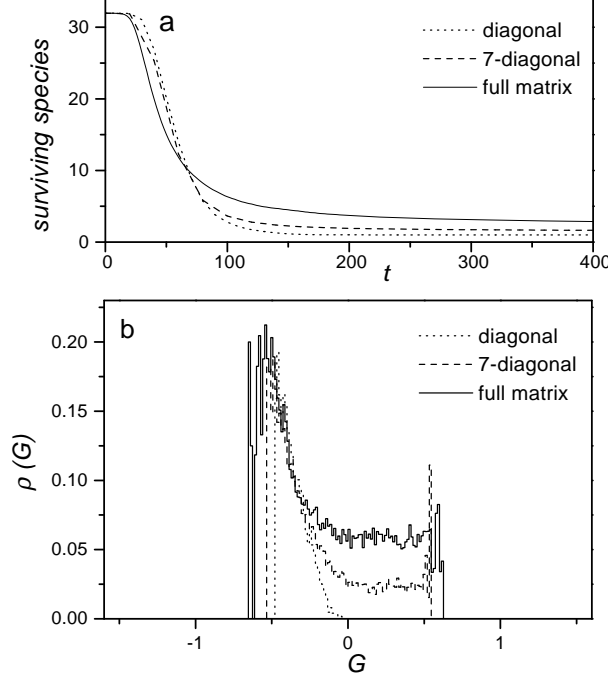


Fig. 4. (a) Number of surviving species as function of time and (b) survival probability $\rho(G)$ for random multi-diagonal matrices, with nonzero elements uniformly distributed on $(-\frac{1}{2}, \frac{1}{2})$.

As a function of G , the fraction of survivals ρ characterizes the probability of surviving for a given species in terms of its ecological attitude toward other species in the system. It is also possible to characterize the survival probability in terms of the average attitude of the ecosystem toward a given species j , which we define as

$$R_j = \frac{1}{N} \sum_i (a_{ji} - a_{ii}) = \frac{1}{N} \sum_i g_{ji}. \quad (4.3)$$

Thus, we have also studied $\rho_R(R)$, the average fraction of surviving species for a given value of R . Figure 6 presents the corresponding results for k -diagonal systems with nonzero elements uniformly distributed on $(-\frac{3}{2}, -\frac{1}{2})$ and different values of k . We observe a monotonous growth of ρ_R , clearly indicating that the probability of surviving for a given species is higher when the remaining species are more altruistic toward it.

Up to now, we have kept the width of the distribution of nonzero elements equal to unity. Here, we briefly analyze the effect of changing this parameter in a particular situation. We consider a 7-diagonal matrix with its nonzero elements distributed uniformly in an interval of width Δ around -1 . Numerical calculations show that the average number of extinctions as a function of time is practically independent of Δ . Figure 7 shows $\rho(G)$ for different values of Δ . As expected, the relevant interval of attitudes grows as the width of the distribution increases.

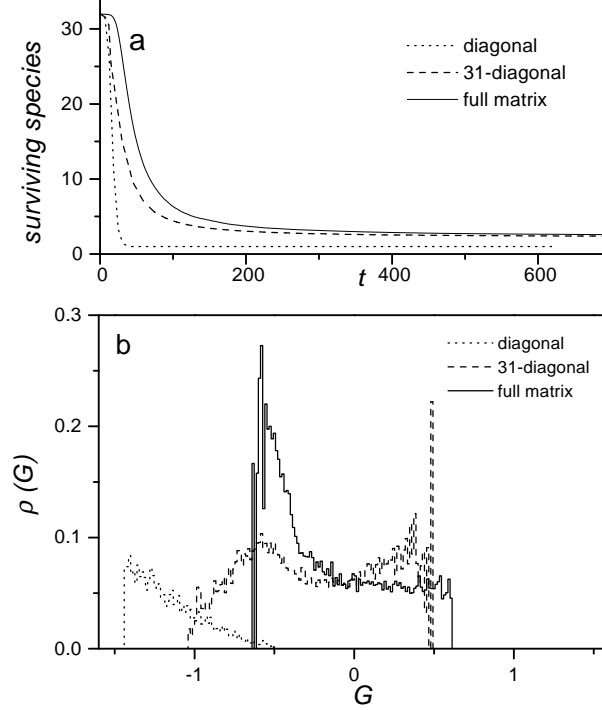


Fig. 5. (a) Number of surviving species as a function of time and (b) survival probability $\rho(G)$, for random multi-diagonal matrices with the nonzero elements uniformly distributed on $(\frac{1}{2}, \frac{3}{2})$. Note that, for 31 diagonals, more than 1/4 of the matrix elements are nonzero. Even though, the number of surviving species is nearly the same as in the full matrix case, which corresponds to $k = 2N - 1 = 63$.

However, no qualitative changes are observed in the profile of ρ .

4.4. Disordered random matrices

Multi-diagonal fitness matrices represent interaction patterns for which the ensemble of species can be ordered in a well-defined sequence, where each species interacts with a few neighbors—besides the global interaction that couples the whole ecosystem. We now turn the attention to systems where the interaction pattern is more disordered than in the multi-diagonal case. We first consider fitness matrices where the diagonal elements are uniformly distributed in a certain interval, while the non-diagonal elements are drawn from the same distribution with probability p and fixed to zero with probability $1 - p$. The diagonal-matrix case corresponds to $p = 0$ and the full-matrix system is attained for $p = 1$.

In Fig. 8 we show results for the average number of surviving species as a function of time, and for the distribution $\rho(G)$, in a system where the nonzero matrix elements are taken from a uniform distribution on $(-\frac{3}{2}, -\frac{1}{2})$, and for different values of p . We find that the distributions $\rho(G)$ for $0 < p < 1$ regularly interpolate

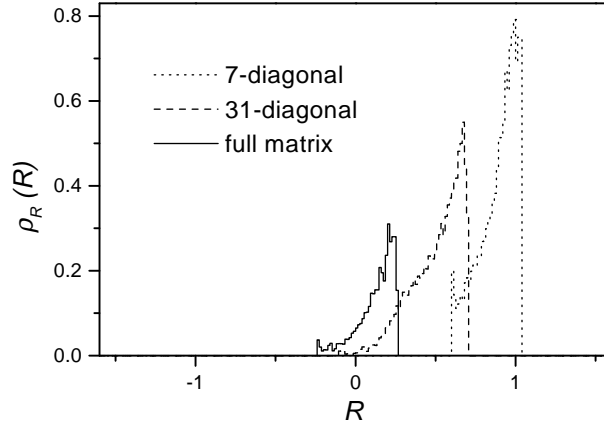


Fig. 6. Fraction of surviving species ρ_R as function of R for a 7-diagonal matrix with nonzero elements uniformly distributed on $(-\frac{1}{2}, \frac{1}{2})$.

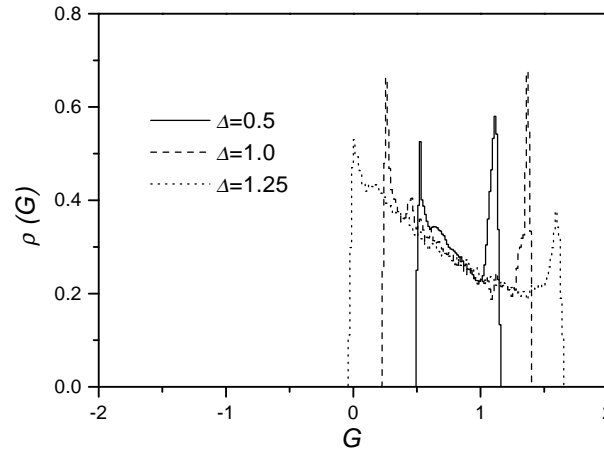


Fig. 7. Survival probability $\rho(G)$ corresponding to 7-diagonal matrices with nonzero elements uniformly distributed on intervals of different widths Δ around -1 .

the two extreme cases. The same feature is found when the nonzero elements are taken from $(-\frac{1}{2}, \frac{1}{2})$ and $(\frac{1}{2}, \frac{3}{2})$.

In Fig. 9 we compare the results for a 3-diagonal system and for a disordered system with probability $p = 2/N = 1/16$, which correspond to the same average number of nonzero matrix elements. It can be seen that the number of surviving species is significantly higher in the disordered system. Note that both systems have the same distribution of attitudes $\langle n(G) \rangle$. This is because, by definition, this function does not depend on the ordering of the interactions, but only on the average number, and distributions, of the nonzero matrix elements. Hence, the difference on the number of extinctions from both systems is a pure consequence of the disorder

of the interactions.

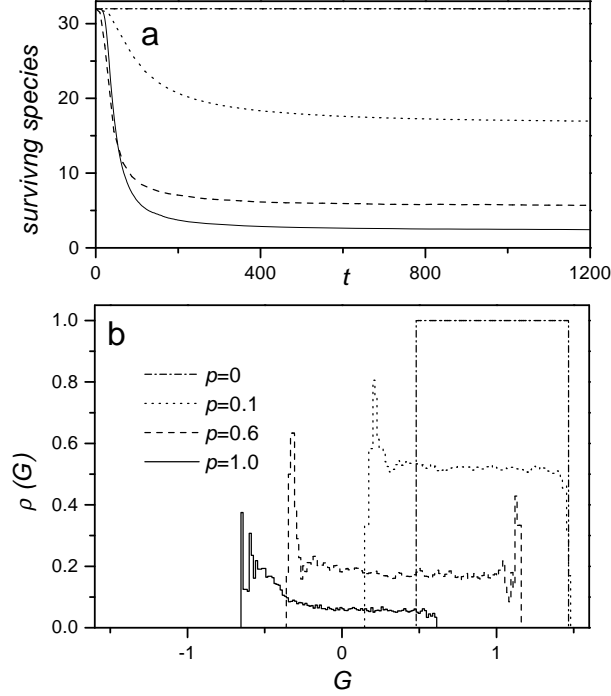


Fig. 8. (a) Number of surviving species as a function of time and (b) survival probability $\rho(G)$, for random matrices with diagonal elements taken from homogeneous distributions on $(-\frac{3}{2}, -\frac{1}{2})$, and non-diagonal matrix elements taken from the same distribution with probability p and fixed as zero with probability $1 - p$. Note that $p = 0$ corresponds to the diagonal matrix case while $p = 1$ corresponds to the full matrix case.

Finally, we study the replicator for a particular set of matrices that constitutes a continuous interpolation between multi-diagonal and disordered matrices. We consider a k -diagonal fitness matrix and, with probability q , we set to zero each element of the $k - 1$ nonzero sub-diagonals. For each of these vanishing elements, we add a new random element outside the multi-diagonal block, $|i - j| > (k - 1)/2$. In this way it is possible, for instance, to transit continuously between the two cases reported in Fig. 9, starting from a 3-diagonal matrix ($q = 0$) and increasing the probability q to approach the disordered case ($q = 1$). Note that the distribution $\langle n(G) \rangle$ does not depend on q , and the only difference between systems with different values of this parameter is the degree of disorder in their interactions. In Fig. 10 we present results for this construction, but starting from a 7-diagonal matrix system. It can be seen that, as the degree of disorder in the fitness matrix grows, the number of survivals increases and the distributions $\rho(G)$ become flatter.

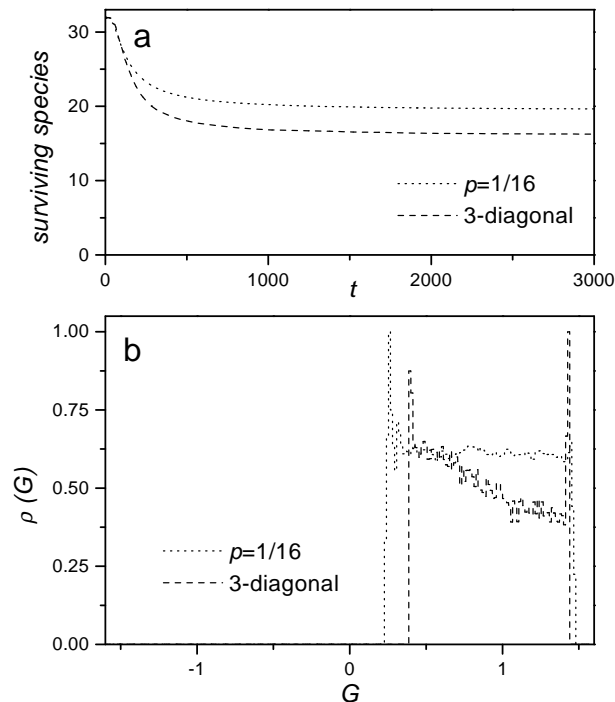


Fig. 9. (a) Number of surviving species as a function of time and (b) survival probability $\rho(G)$, for a 3-diagonal matrix with nonzero elements uniformly distributed on $(-\frac{3}{2}, -\frac{1}{2})$ and for a random disordered matrix with diagonal elements taken from the same distribution, and non-diagonal elements taken with probability p from the same distribution and fixed as zero with probability $1 - p$.

5. Conclusions

In this paper we have presented a statistical study of survival and extinction in the replicator model with linear fitness, exploring in particular the effect of the pattern of interactions in the ecosystem. We have selected a set of interaction patterns and fitness matrices that is expected to provide a representative (though not complete) sample of the different possible situations found in complex model ecosystems. Through the definition of the mean attitude of a species, we give a compact characterization of its ecological behavior, avoiding the problem of dealing with the detailed information involved in the fitness matrix. Our analysis has been focused on the study of the evolution of the number of surviving species for different interaction patterns, and on the determination of the survival probability as a function of the mean attitude. In the following, we summarize and comment our main conclusions.

Concerning the number of surviving species in a given population, we have found that, in all cases, it increases as the mean attitude of the whole ensemble of species shifts to larger values. In other words, survival probabilities are higher in altruistic

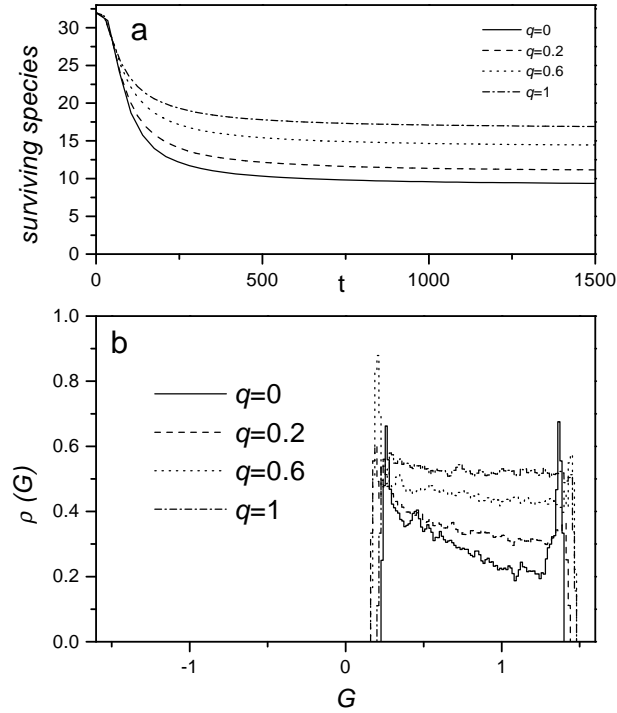


Fig. 10. (a) Number of surviving species as a function of time and (b) survival probability $\rho(G)$, for a 7-diagonal system that is being disordered by increasing the probability q . The nonzero matrix elements are uniformly distributed on $(-\frac{3}{2}, -\frac{1}{2})$.

populations. This property is clearly observed for multi-diagonal and disordered matrices, and for different distributions of the nonzero matrix elements.

The survival probability grows also with the disorder of the fitness matrix, as illustrated by Figs. 10 and 7, where we have compared the results for populations with different degrees of disorder in their interactions, but equal distributions of the mean attitude. In contrast with the case of multi-diagonal fitness matrices, where the number of interaction links is the same for all species, for disordered matrices there is a chance that the ecosystem becomes divided into weakly interacting subsystems. Within one of such subsystems, each species interacts with a relatively smaller population and its survival probability thus increases.

Once the fitness matrix of a population is fixed, we find that the survival probability is higher for the most extreme attitudes. In most situations, in fact, species with the lowest and largest mean attitudes –i. e., the most egoistic and the most altruistic, respectively– have better chances of surviving. Some remarkable exceptions have been found, however, where the egoistic extreme is not a good option, and an intermediate mean attitude maximizes the survival probability (see Fig. 5). In contrast, the altruistic extreme has always been found to have a relative high chance, if not the highest, of surviving.

Let us finally stress that the present analysis has explored only a class of possible interaction patterns in the multi-species replicator model, with specific choices for the structure of the fitness matrix and the distribution of its elements. The possibility is open for the consideration of much more general situations, approaching the statistical description of large real ecosystems with arbitrary, even highly complex, food-web structures.

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